Holoplanktonic mollusks off western Baja California during the weak El Niño 2006-07 and further transition to La Niña

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Abstract: There are few studies on pelagic mollusks from the California Current, despite their ecological importance and vulnerability to climate change (*e.g.,* ocean acidification and hypoxia). We analyzed abundances of holoplanktonic mollusks during three years (2006-2008) along a transect-line parallel to the Baja California coast. The main differences in physical factors were increasing temperature and salinity from north to south, and lower dissolved oxygen concentration south of Punta Eugenia (28°N). The lowest oxygen concentrations occurred in summer, with hypoxic conditions (< 0.5 ml $\cdot$ L^{-1}) in the upper 100 m depth at some locations. Planktonic mollusk abundance did not differ along the latitudinal gradient, excepting *Desmopterus pacificus* Essenberg, 1919 and individuals from the genus *Pterotrachea* Forskal, 1775. In contrast, the temporal variability was high, mainly in a seasonal scale but also among years. The influence of El Niño 2006-2007 and La Niña 2007-2008 were evident by a sharp increase of *Corolla spectabilis* Dall, 1871 in April 2007 during the El Niño-La Niña transition. During 2008, pelagic mollusks remained with moderate abundance in winter-spring despite the high chlorophyll concentrations recorded (up to 3.26 mg $\cdot$ m^{-3}). Subsequently, during the relaxation of a first pulse of La Niña in July 2008, there was a rebound in the abundance of the heteropod *Atlanta* Lesueur, 1817. and individuals in the Order Gymnosomata. The oxygen gradient inversely influenced mollusk abundance in most of the genera (*Clio* Linnaeus, 1767, *Limacina* Bosc, 1817, *Atlanta*, and *Firoloida* Lesueur, 1817) and the order Gymnosomata, but for *Cavolinia* Abildgaard, 1791, *Creseis* Rang, 1828, *Desmopterus*, and *Pterotrachea*, the salinity gradient was more influential. Therefore, holoplanktonic mollusks genera were useful indicators of climatic variability.

Key words: zooplankton, pteropods, heteropods, hypoxia, California Current

Holoplanktonic mollusks are an ensemble of gastropod species which have developed particular adaptations to pelagic life such as a reduced shell composed of aragonite (Lalli and Gilmer 1989). Holoplanktonic mollusks can be placed into two groups, pteropods and heteropods, both possessing a larval phase which includes a protoconch, but in the adult phase, some species develop a definitive shell while other lose the shell. Organisms in the suborder Pseudothecosomata possess a hyaline shell, in which the aragonite has been replaced by an organic matrix. This light-weight pseudo-conch enables the development of such large sized pteropods as *Corolla spectabilis*, whose pseudoconch measures up to 80 mm length and the soft body has a swimming disk of 120 mm diameter (Lalli and Gilmer 1989). This allows *C. spectabilis*, the largest phytoplanktofagous pteropod, to collect a large amount of food particles via mucous nets (Gilmer and Harbison 1986). Naked pteropods (Gymnosomata) and Heteropoda are carnivores.

Hypoxic conditions combined with acidification make pelagic mollusks doubly vulnerable to climate change (Maas *et al.* 2012). First, the fragility of aragonite shells make them particularly vulnerable to ocean acidification, due to the increase of atmospheric CO_2 (Zhang *et al.* 2011). Calcareous organisms depend of $CaCO_3$ oversaturation in the seawater to avoid the dissolution of their exoskeletons and shells.

Acidification also affects physiological processes in the open circulatory system of invertebrate organisms that need an acid-base equilibrium of corporal fluids (Fabry *et al.* 2008, Whiteley 2011). The second problem derived from the climate change, is the decrease of oxygen concentration in the sea and specifically the expansion of the minimum oxygen zones (MOZ; Paulmier and Ruiz-Pino 2009). The MOZ occur at relatively shallow depths where the biological productivity is high and the vertical carbon flow is intense, such as in the eastern tropical Pacific.

These problems are particularly threatening in eastern boundary upwelling ecosystems where the upwelled water is rich in CO_2. In the California Current System (CCS), the presence of low pH water has been documented in the coastal shelf of California and Baja California (Feeley *et al.* 2008, Gruber *et al.* 2012), as well as a deoxygenating process probably related with the enhancement of the California Undercurrent (Bograd *et al.* 2015) and the generation of subsurface eddies (Jerónimo and Gómez-Valdés 2007).

Because planktonic mollusks are good indicators of acidification and hypoxia, it is important to monitor their abundance. In the region off southern California, Ohman *et al.* (2009) analyzed the variability in abundance of thecosome and heteropod mollusks between 1951-2008, but did not find evidence of a decrease in mollusk abundances as would be

expected by the incidence of aragonite subsaturated water (Feeley *et al.* 2008). However, another study in the North Pacific off Vancouver, Canada, showed a decrease in *Limacina* species between 1979 and 2011 (Mackas and Galbraith 2012). Thinning of shells was observed in *Limacina helicina* (Phipps, 1774) collected during strong upwelling pulses (Bednarsěk *et al.* 2014). In contrast to the North Pacific, there is scarce information in the region off Baja California about holo-planktonic mollusks other than their distribution (McGowan 1967, Sánchez-Hidalgo 1989, 1994). In order to deepen the understanding in temporal changes in the abundance of these organisms in the subtropical region of the California Cur-rent, the present study address interannual changes along a latitudinal transect during a three year period (2006-2008) when a weak El Niño took place in 2006-2007 followed by La Niña 2007-2008. We expected to find changes in mollusk abundance related to environmental factors as temperature, salinity, dissolved oxygen and chlorophyll concentration.

MATERIALS AND METHODS

We examined planktonic mollusks from nine cruises performed by "Investigaciones Mexicanas de la Corriente de California" (IMECOCAL). Selected stations ran along a latitudinal transect located between 60-90 km from the coast, and passed through the nucleus of the California Current (Fig. 1). Surveys were performed in winter, spring, and summer of 2006–2008 (sampling dates are shown in Table 1). To assess environmental conditions, a CTD/rosette was lowered into the ocean, taking water from six depths (0, 20, 50, 100, 150, and 200 m), to further analyses of dis-solved oxygen and chlorophyll *a*. The oxygen was measured with microwinkler titration. The chlorophyll was determined using one liter of sea water filtered with Whatman GF/F filters of 0.7 µm of pore-size. Filters were kept in liquid nitrogen to further analysis with a fluorometer following to Venrick and Hayward (1984).

Zooplankton was collected with a bongo net (0.5-mm of mesh-width, 0.71-m of mouth diameter), towed obliquely between the surface and 210 m depth. The volume of water filtered was measured with a flowmeter in front of the net, and samples were fixed with 4% formaldehyde buffered with sodium borate. The number of samples selected was 10–12 per cruise, with the exceptions of April 2007 and April 2008 when only 8 samples were collected. In the laboratory, samples were split to ½ or ¼ and mollusks were identified and counted in the fraction. Thecosomata and Heteropoda were identified mainly to genera and in some cases to species, while the Gymnosomata only to order, based in taxonomic keys by McGowan (1968), Van der Spoel *et al.* (1997), Richter and Seapy (1999), and Van der Spoel and Dadon (1999).

Data analysis

Abundance data were not nor-mally distributed and were trans-formed using the function *log x + 1*. Transformed data from each genus were compared between stations per-taining to north and south sections of the transect-line with the Sudent´s *t* test, taking Punta Eugenia (28° N) as the separation point. Temporal vari-ability was compared with two factor
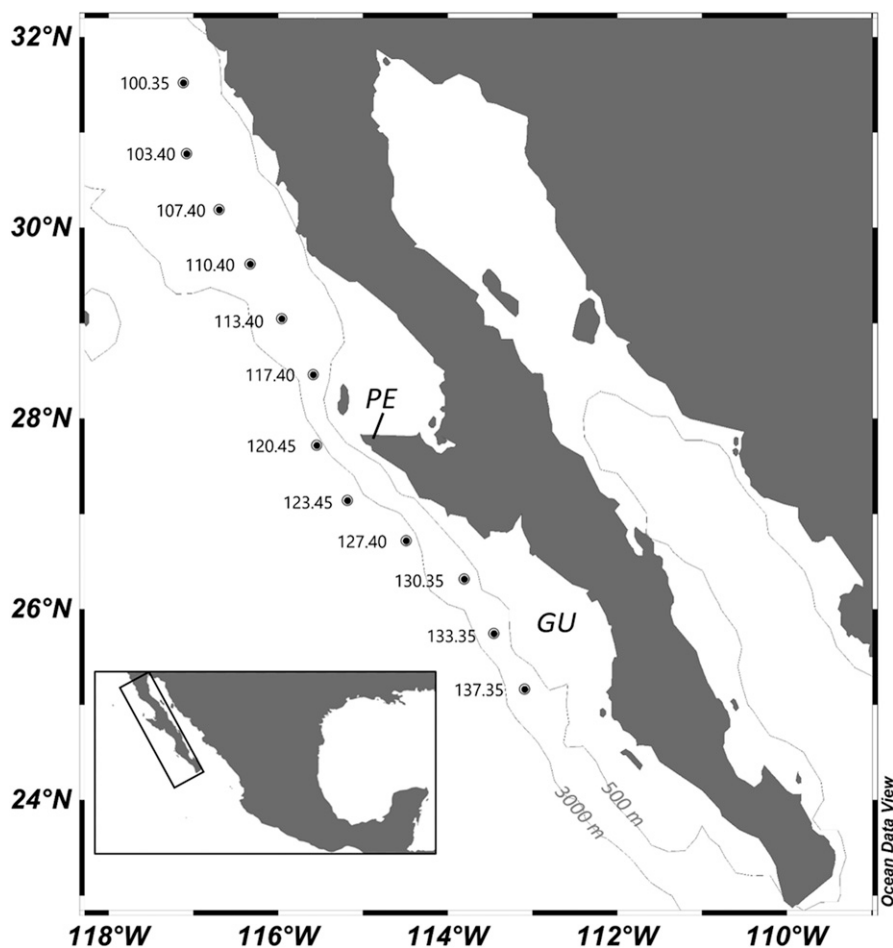

Figure 1. Latitudinal transect off Baja California showing the number of sampling stations. (PE) Punta Eugenia, (GU) Gulf of Ulloa.

Table 1. Environmental variables used in multiple regression analysis. The mean and standard deviations by cruise is shown. The geometric mean was used for integrated chlorophyll in the upper 100 m depth. The gradient is defined as the difference between values of 10 and 100 m depth. * The variable S_{200} was dropped from the regression analysis due to is redundant with T_{200}.

Variables	Code	Cruises								
		0602 5–25 Feb 2006	0604 19 Apr–1 May 2006	0607 7–25 Jul 2006	0701 23 Jan–10 Feb 2007	0704 26 Apr–6 May 2007	0708 25 Aug–13 Sep 2007	0801 23 Jan–11 Feb 2008	0804 16 Apr–1 May 2008	0807 14 Jul–2 Aug 2008
10 m depth temperature (°C)	T_{10}	15.6 ± 0.7	16.4 ± 0.5	20.6 ± 1.4	17.1 ± 1.5	15.5 ± 0.3	20.5 ± 1.7	15.5 ± 1.1	15.8 ± 1.0	19.5 ± 1.4
10 m depth salinity (psu)	S_{10}	33.5 ± 0.1	33.5 ± 0.1	33.6 ± 0.2	34.0 ± 0.4	33.6 ± 0.1	33.7 ± 0.1	33.7 ± 0.2	33.6 ± 0.1	33.6 ± 0.2
10 m depth oxygen (ml L^{-1})	O_{10}	5.6 ± 0.2	4.9 ± 0.2	4.4 ± 0.1	5.8 ± 0.2	5.5 ± 0.1	5.1 ± 0.3	5.5 ± 0.2	6.1 ± 0.3	6.7 ± 1.0
200 m depth temperature (°C)	T_{200}	9.8 ± 0.6	9.8 ± 0.7	10.4 ± 1.2	10.7 ± 0.7	9.6 ± 0.8	10.2 ± 0.9	10.2 ± 0.7	9.6 ± 0.9	10.7 ± 0.9
200 m depth salinity (psu) *	S_{200}	34.3 ± 0.1	34.3 ± 0.2	34.3 ± 0.3	34.4 ± 0.2	34.3 ± 0.2	34.3 ± 0.2	34.3 ± 0.2	34.3 ± 0.2	34.5 ± 0.2
200 m depth oxygen (ml L^{-1})	O_{200}	1.5 ± 0.5	1.1 ± 0.5	1.1 ± 0.9	1.2 ± 0.7	1.2 ± 0.6	1.2 ± 0.8	1.1 ± 0.7	1.4 ± 0.7	1.6 ± 0.8
Thermal gradient (°C)	dT	4.6 ± 0.8	5.7 ± 0.8	8.8 ± 2.0	4.6 ± 1.1	4.8 ± 0.7	8.9 ± 1.5	4.0 ± 0.7	5.1 ± 0.8	8.1 ± 1.9
Saline gradient (psu)	dS	0.4 ± 0.2	0.3 ± 0.2	0.3 ± 0.4	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.3	0.3 ± 0.1	0.4 ± 0.2	0.3 ± 0.3
Oxygen gradient (ml L^{-1})	dO	2.7 ± 0.9	2.1 ± 0.8	2.0 ± 1.4	2.8 ± 0.9	2.9 ± 0.9	2.6 ± 1.6	3.2 ± 0.7	3.6 ± 1.0	3.4 ± 2.1
Integrated chlorophyll (mg m^{-2})	ICh	31 ± 14	25 ± 19	34 ± 31	61 ± 25	51 ± 32	36 ± 16	103 ± 29	112 ± 59	79 ± 85

Analysis of Variance (month and year). Following significant ANOVA results, Tukey tests were used to determine differences among months and years.

In addition, multiple regression analysis was run for each taxonomic group to test which environmental variables were good predictors of genera abundance. The stepwise forward procedure was applied considering the following ten variables: temperature at 10 m (T_{10}), salinity at 10 m (S_{10}), oxygen at 10 m (O_{10}), temperature at 200 m (T_{200}), salinity at 200 m (S_{200}), oxygen at 200 m (O_{200}), thermal gradient (dT), saline gradient (dS), oxygen gradient (dO), and integrated chlorophyll (ICh). The gradient is defined as the difference between values of 10 and 100 m depth. Chlorophyll data were log-transformed.

The collinearity among independent variables was explored using principal component analysis. The correlation matrix showed high values for the pair S_{200} and T_{200} (r = 0.908) and the pair T_{10} and dT (r = 0.917). However, the inverse covariance matrix only showed values out of range for S_{200}, and therefore was dropped from the multiple regression analysis.

RESULTS

Environmental conditions

Sea surface temperature (SST) ranged between 13.8 and 23.5 °C during the study period. Lower temperatures occurred in winter and spring, though SST from January 2007 was 1.5-2 °C warmer compared to winters of 2006 and 2008 (Table 1), due to El Niño 2006-2007. Spring SST was similar in the three years, with mean SST (± standard deviation) between 15.5 ± 0.3 and 16.4 ± 0.5 °C. In summer, SST increased around 4 °C in relation to spring, remaining cooler in 2008 (19.5 ± 1.4 °C), showing the signal of La Niña 2007-2008. The thermocline was deeper in winter, down to 50-60 m in 2006 and 2008 but 80-90 m in 2007. In later months, the depth of thermocline became shallower, 30-50 m in April of 2006-2008 and 10-30 m in summer of 2007-2008 (Fig. 2). This resulted in a stronger thermal gradient during summer. Upwelling activity was evident by low temperatures around of Punta Eugenia, more evident in April 2006. Through the study period, the water column presented strong stratification in the northern part of the transect contrasting with the southern part where subsurface waters were warmer.

Sea surface salinity (SSS) showed interannual variability higher than that recorded seasonally. A surface layer below 34 practical salinity units (psu) was observed always associated to Subarctic Water, but during 2006 this layer was thicker, reaching down 100-150 m depth (Fig. 3). In January 2007, the SSS increased, particularly south of Punta Eugenia, with values of 34.0-34.5 psu associated to the Subtropical Water mass, resulting in a negative value for the salinity gradient
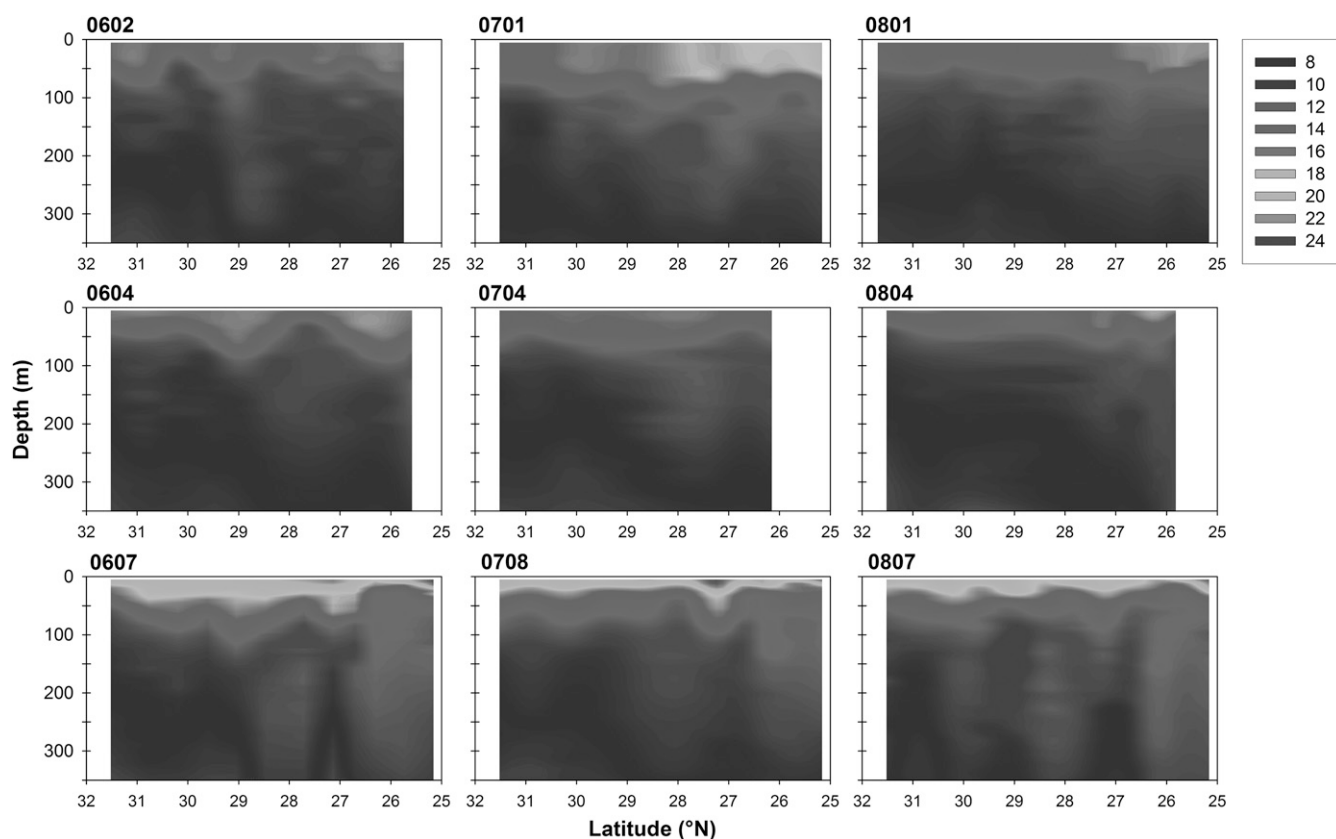
Figure 2. Vertical section of temperature (°C) along a transect parallel to the western coast of Baja California during 2006-2008. In this and further figures 3-5, left panels correspond to cruises performed in February, April, and July of 2006 (0602, 0604, 0607); central panels to January, April, and August of 2007 (0701, 0704, 0708); and in the left are January, April, and July of 2008 (0801, 0804, 0807).

Therefore the absolute value of the salinity gradient is considered (Table 1). The presence of high salinity below 150-200 m, was a general pattern in the study region, with values of 34.3-34.7 psu, associated to the Subsurface Equatorial water. This equatorial water occupied a higher volume in the southern stations with maximum values in summer.

Surface dissolved oxygen concentrations ranged from 4.4 to 6.7 ml · L^{-1} during the study period (Table 1), with the lowest values observed in July 2006 associated with the 2006-2007 El Niño. The water column in the northern zone remained consistently better oxygenated than at south (Fig. 4). Low oxygen concentrations were recorded below 100-150 m depth, but in some points there were hypoxic conditions (<0.5 ml · L^{-1}), such as in July 2006 off the Gulf of Ulloa (25.8°N) above of 65 m depth. Seasonal variability was low, and interannual variability higher, with means of 5.0, 5.5, and 6.1 ml · L^{-1} for 2006, 2007, and 2008 respectively, which resulted in higher oxygen gradient in 2008 (Table 1).

Chlorophyll concentrations were highly variable in the euphotic zone. In some cruises, a north-south trend was observed in the chlorophyll maximum depth, *e.g.,* April 2007

(Fig. 5). As would be expected, chlorophyll was higher around Punta Eugenia, particularly in spring associated to coastal upwelling. The integrated chlorophyll in the upper 100 m, showed interannual variability with the lowest values in 2006 and the highest in 2008 (Table 1). In contrast, the seasonal variability was weak (Table 1).

Holoplanktonic mollusks

We found eight pteropod genera from the order Thecosomata and four heteropod genera, now considered part of the superfamily Pterotracheoidea (Bouchet and Rocroi 2005). Pteropods from the order Gymnosomata were not identified to genera (Table 2). The presence of mollusks in samples was variable but true shelled pteropods (Euthecosomata) were the most frequently found excepting *Cuvierina* Boas, 1886. *Cuvierina* was only recorded in four cruises with frequency of 9-33%. Other pteropods (Pseudothecosomata and Gymnosomata) occurred in less than 50% of the samples. With regard to the heteropods, *Atlanta* Lesueur, 1817 was the genus with highest presence, recorded in 73-100% of the samples, excepting in the spring of 2008 (38%). *Firoloida*
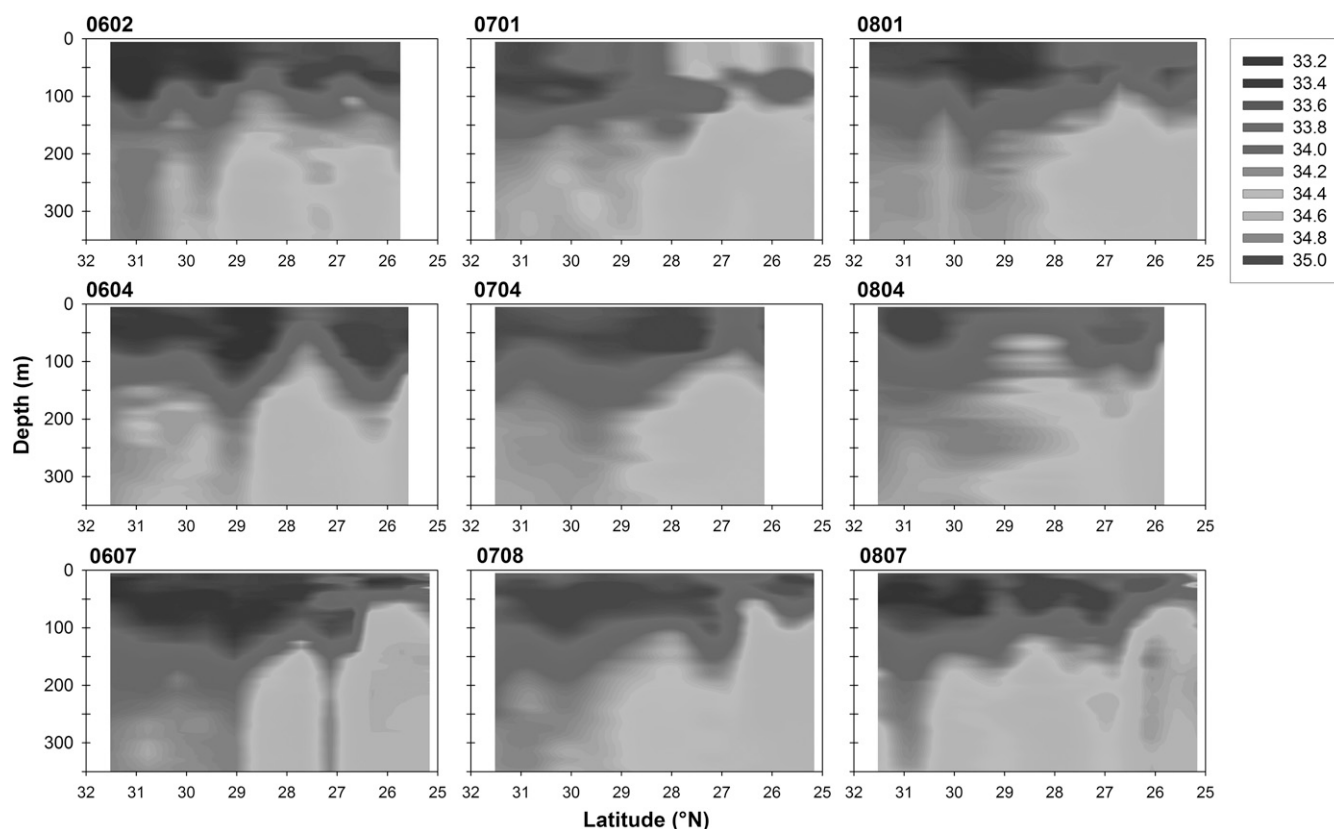
Figure 3. Vertical section of salinity (ups) along a transect parallel to the western coast of Baja California during 2006-2008.

Lesueur, 1817 was also common, present in 9-58% of the samples, followed by *Pterotrachea* Forskal, 1775 (0-42%) and *Carinaria* Lamarck, 1801 (0-45%).

Regional variability

Abundance of Euthecosomata was typically higher than other pteropods with a geometric mean (GM) = 87 ind/1000 m^3, while the Pseudothecosomata and Gymnosomata had 4.5 and 0.5 ind/1000 m^3 respectively. Euthecosomata pteropods were not evenly distributed along the transect (Fig. 6). Across our transect *Limacina* Bosc, 1817 and *Creseis* Rang, 1828 were similarly abundant (~ 70 ind/1000 m^3; Table 2). Based on the GM, *Limacina* was 47% of pteropods, followed by *Creseis* (32%), *Cavolinia* Abildgaard, 1791 (11%), *Clio* Linnaeus, 1767 (8%), *Peracle* Pelseneer, 1888 (2%) and <1% for *Cuvierina*. Relative abundance of *Limacina* was higher in the north region during the winter 2006, but this pattern was not consistent in other periods. *Creseis* did also not present consistent distribution, dominating in the south during February 2006 and April 2008, but in the north during April 2007 and January 2008, or along transect in the rest of cruises (Fig. 6). *Cavolinia* was in low abundance during 2006 and increased in winter-spring of 2007 and again in winter 2008. *Clio* was

sporadically abundant in southern stations. However, the statistical comparison between regions did not present significant differences in the abundance of euthecosomatous genera.

In Pseudothecosomata, the three genera had modest abundances with a global geometric mean below 2 ind/1000 m^3 (Table 2). Only *Desmopterus pacificus* Essenberg, 1919, had a significant regional difference (t = 2.16, p = 0.033) with higher abundance north of Punta Eugenia.

Among the heteropods, *Atlanta* was the genus more abundant with a global GM of 32 ind/1000 m^3 (Fig. 7, 8j). The other genera had low abundance and were mainly represented by one species: *Firoloida desmarestia* Lesueur, 1817, dominating in January 2007 at several stations; *Pterotrachea coronata* Forsskål in Niebuhr, 1775, was relatively influential in August 2007 and April 2008; and *Carinaria japonica* Okutani, 1955, sporadically appearing in samples. The regional comparison only was significant for *Pterotrachea*, which was more abundant in the south (t = -2.21, p = 0.030).

Temporal Variability

All Euthecosomata displayed seasonal differences, excepting *Cuvierina* (Table 3). There was a significant interaction
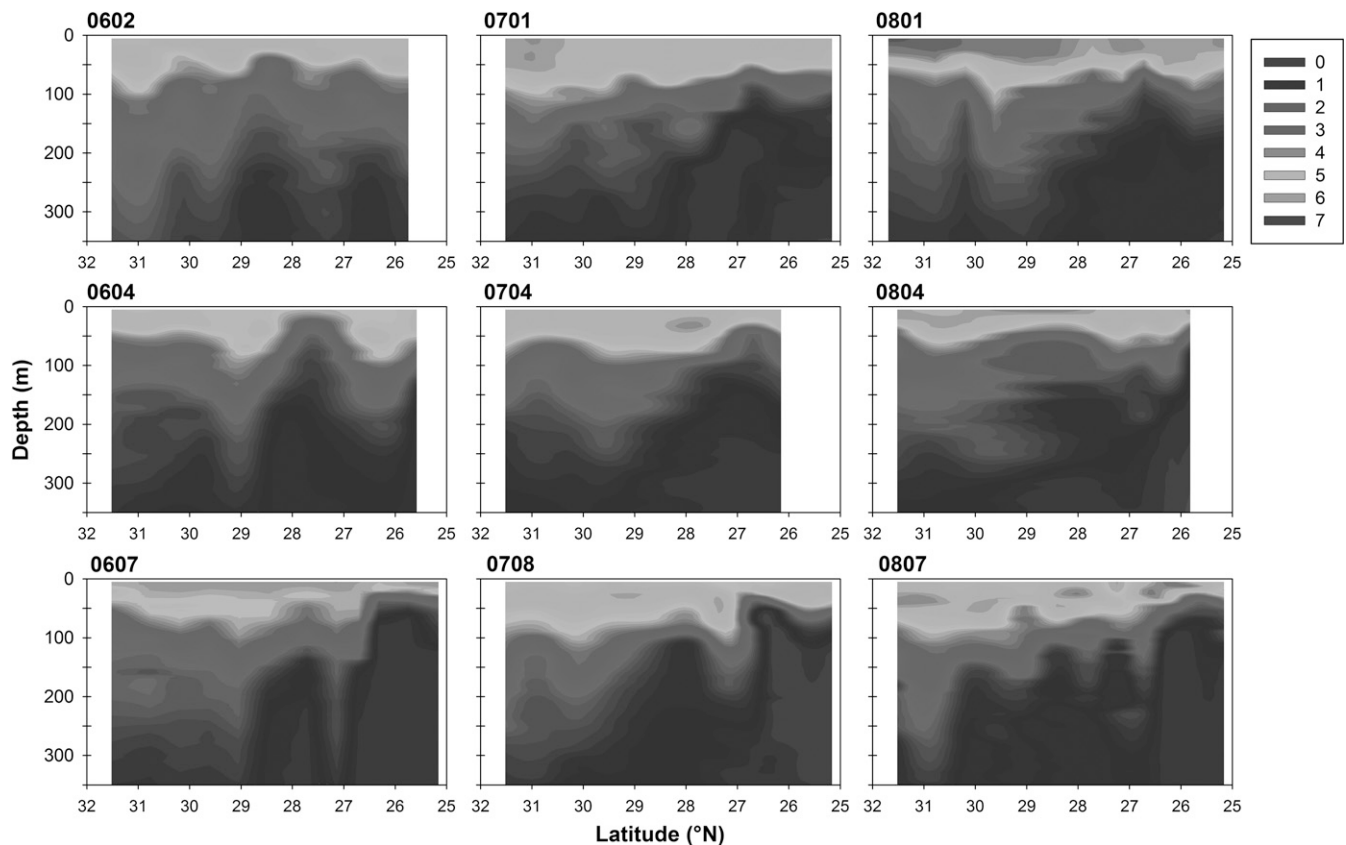
Figure 4. Vertical section of dissolved oxygen (ml · L^{-1}) along a transect parallel to the western coast of Baja California during 2006-2008.

between month and year (F = 3.90, p = 0.006), but there were not pairwise differences with the Tukey test (p > 0.05) due to the total absence of *Cuvierina* in five cruises (summer 2006, winter-spring 2007, and spring-summer 2008). The scarce abundance of *Cuvierina* make difficult to establish a definite pattern (Fig. 8d). The most abundant, *Limacina*, showed monthly differences and *a posteriori* comparisons indicated an increase in summer relative to spring, from a GM = 11 ind/1000 m^3 to 42 ind/1000 m^3 (p = 0.002; Fig. 8e). *Creseis* also increased from winter to summer (p = 0.028; Fig. 8c). In contrast, a decrease in abundance of 76-82% was observed from spring to summer in *Cavolinia* (p =0.022; Fig. 8a) and *Clio* (p = 0.003; Fig. 8b).

Corolla spectabilis Dall, 1871, was the most abundant genus of the Psedothecosomata. Its abundance was generally low (2 ind/1000 m^3) except during spring 2007 when its abundance increased to 29 ind/1000 m^3 (Fig. 8f, Table 3). ANOVA was significant for both factors but the interaction between month and year revealed that only spring 2007 was different to the rest of cruises (F = 10.55, p < 0.001). Abundance of *Desmopterus pacificus* was consistently low during the study period (Fig. 8g, Table 3). In relation to

Peracle, only seasonal differences were observed, with maximal abundance in summer (Fig. 8h).

Gymnosomata were in low abundance through the study period (<2 ind/1000 m^3) except in summer 2008 when increased to 4 ind/1000 m^3 (Fig. 8i, Table 3). During 2006 and 2007 the higher abundance occurred in spring, while in 2008 were absent in spring and peaked in summer (p = 0.023) probably due to cool temperature during La Niña.

The heteropod *Atlanta* had seasonal and interannual differences (Table 3, Fig. 8j). This genus was more abundant in summer, reaching a GM = 75 ind/1000 m^3 while in winter and spring was 73-76% lower in 2006 and 2008. However, in 2007 the abundance remained high from winter to summer. Comparing among years, *Atlanta* had the highest abundance in 2007 with a GM = 73 ind/1000 m^3 (F = 7.91, p = 0.001). However, month-year interaction showed differences associated to a significant decrease of *Atlanta* in spring 2008 (GM = 3 ind/1000 m^3) followed by a rebound next summer to 137 ind/1000 m^3 (p < 0.001). *Firoloida* showed a similar pattern of seasonal and interannual differences (Table 3, Fig. 8l). *Pterotrachea* abundance only presented interannual differences (F = 4.41, p = 0.015) with abundance in 2007 higher
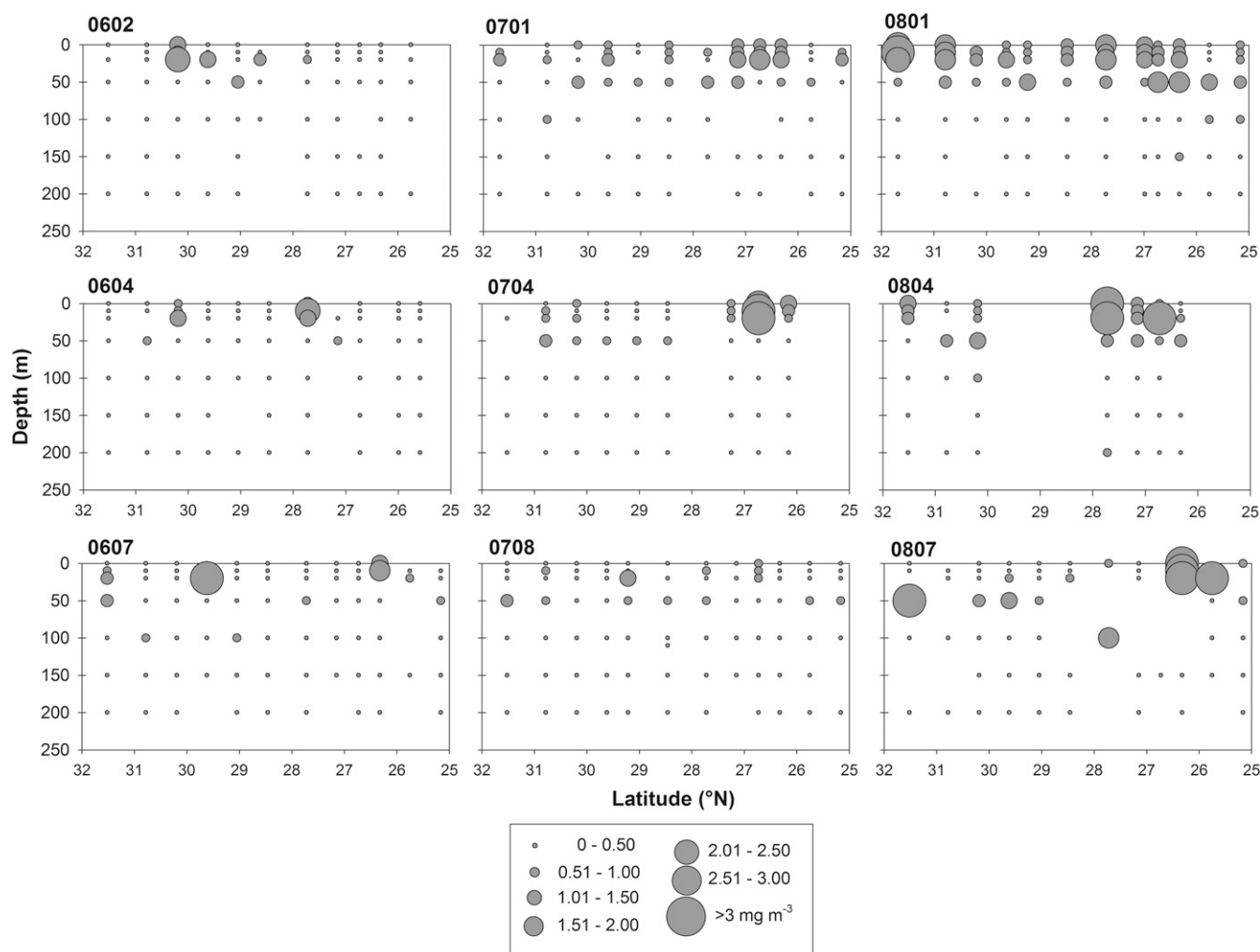
Figure 5. Vertical section of chlorophyll (mg · m^{-3}) along a transect parallel to the western coast of Baja California during 2006-2008.

than in 2006 (p = 0.009, Fig. 8m). *Carinaria* was absent in two cruises (July 2006 and April 2008), and scarce in the rest, resulting difficult establishing a temporal pattern (Fig 8k).

Biophysical coupling

Multiple regression analysis applied to each genus of holoplanktonic mollusks was significant excepting for *Cuvierina*, *Corolla*, and *Carinaria* (Table 4). However, for the rest of taxa the explained variance was low, with R^2 ranging from 0.151 to 0.311. The number of environmental variables selected in regression equations was between two and seven. The variables selected by a higher number of genera were T_{10}, S_{10}, T_{200}, dT, dS, and dO. The relative contribution of each independent variable in the prediction of the dependent variable is expressed by the coefficient and each one have an associated probability. For example, the variable dO presented statistically

significant regression coefficients for *Clio* (t = -2.6, p = 0.010), Gymnosomata (t = -3.07, p = 0.003), *Atlanta* (t = -3.0, p = 0.004), and *Firoloida* (t = -2.5, p = 0.014); but not for *Limacina*, *Peracle*, and *Pterotrachea* (Table 4). The inverse relation between dO and abundances of these mollusks may indicate a lower tolerance to low oxygen concentration in the water column. This is also consistent with positive significant O_{10} coefficients for *Peracle*, Gymnosomata, and *Atlanta* (Table 4), indicating higher abundance in well oxygenated surface water.

Thermal and saline gradients were important in some genera of pteropods, and were inversely related to abundance of *Cavolinia* (p < 0.001 in both cases), *Clio* (p = 0.002 for dT), *Creseis* (p = 0.045 for dS), and *Desmopterus* (p < 0.001 for dS). However, other mollusks had a positive relation between abundance and dT, as *Peracle* (t = 2.8, p = 0.007) and

Table 2. Number of samples with presence of holoplanktonic mollusks by cruises and global abundance (ind/1000 m3) based on the mean and geometric mean (GM). Total number of analyzed samples indicated in brackets. (*) Replace the previous Order Heteropoda. Taxonomic classification based in the World Register of Marine Species (http://www.marinespecies.org).

| Taxa	Cruise									Abundance	
	0602 (11)	0604 (11)	0607 (12)	0701 (12)	0704 (8)	0708 (12)	0801 (12)	0804 (8)	0807 (12)	Mean	GM
Order Thecosomata											
Suborder Euthecosomata											
Cavolinia Abildgaard, 1791	7	8	4	10	7	7	10	4	3	23	5.2
Clio Linnaeus, 1767	5	8	3	10	6	4	6	4	3	17	3.4
Creseis Rang, 1828	7	8	10	8	8	11	7	3	12	70	15.5
Cuvierina Boas, 1886	1	2	0	0	0	4	2	0	0	1	0.2
Limacina Bosc, 1817	11	10	12	12	5	11	11	8	12	71	24.1
Suborder Pseudothecosomata											
Corolla spectabilis Dall, 1871	0	2	5	2	8	5	1	2	3	10	0.9
Desmopterus pacificus Essenberg, 1919	1	5	6	4	5	2	2	1	6	5	1.2
Peracle Pelseneer, 1888	1	5	3	2	1	5	4	1	9	5	1.2
Order Gymnosomata	1	5	2	0	2	1	1	0	7	4	0.5
Order Littorinimorpha											
Superfamilia Pterotracheoidea*											
Atlanta Lesueur, 1817	8	8	12	12	7	11	12	3	12	95	32.1
Carinaria Lamarck, 1801	5	1	0	1	3	4	2	0	1	1	0.4
Firoloida desmarestia Lesueur, 1817	4	1	2	8	4	7	4	2	4	14	1.8
Pterotrachea Forskal, 1775	0	0	2	3	2	5	0	2	3	3	0.5
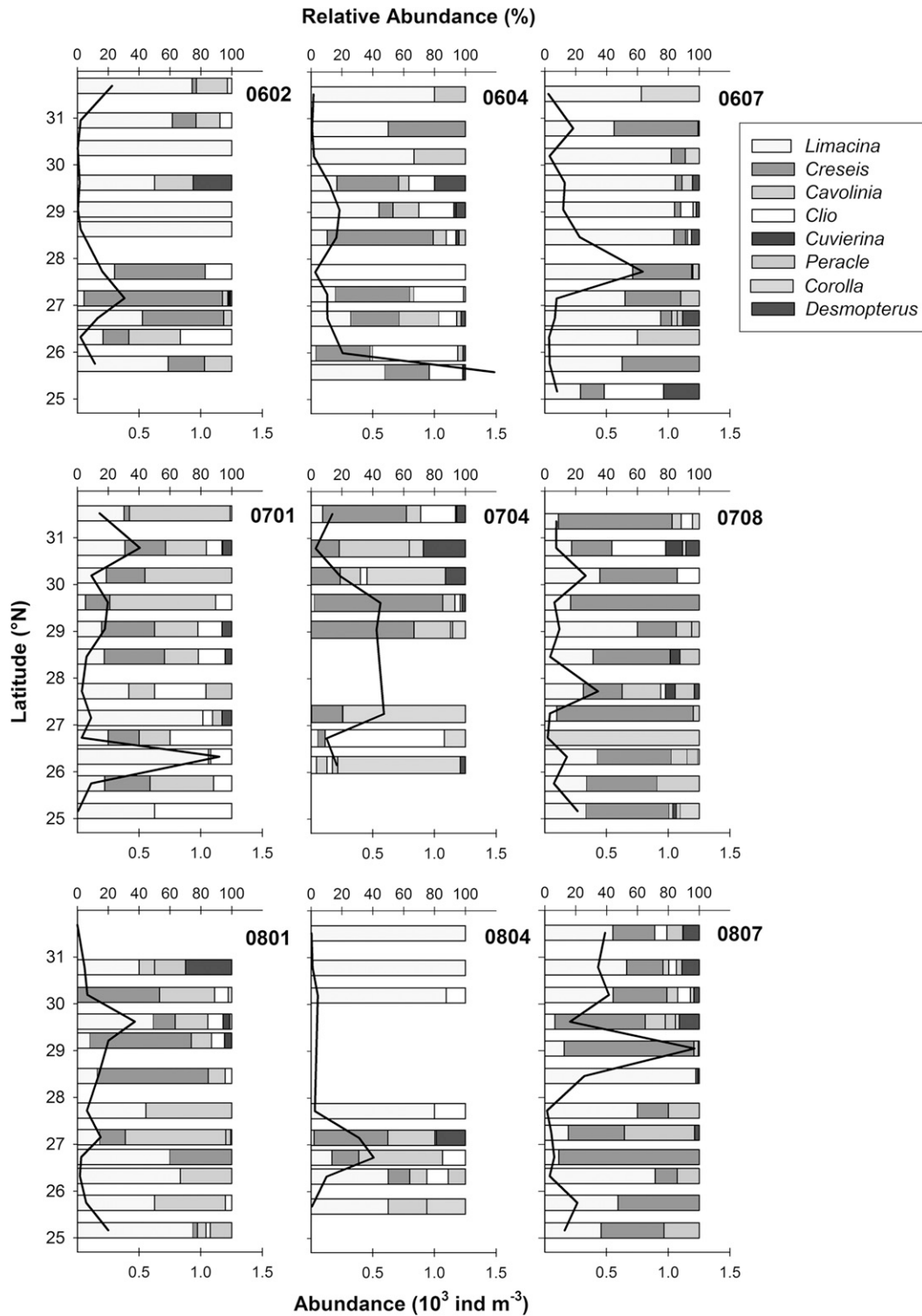
Figure 6. Thecosomata pteropods distribution along a latitudinal transect off the Baja California western coast during 2006-2008. Colors in bars represent relative abundance by genera and solid line is total absolute abundance.
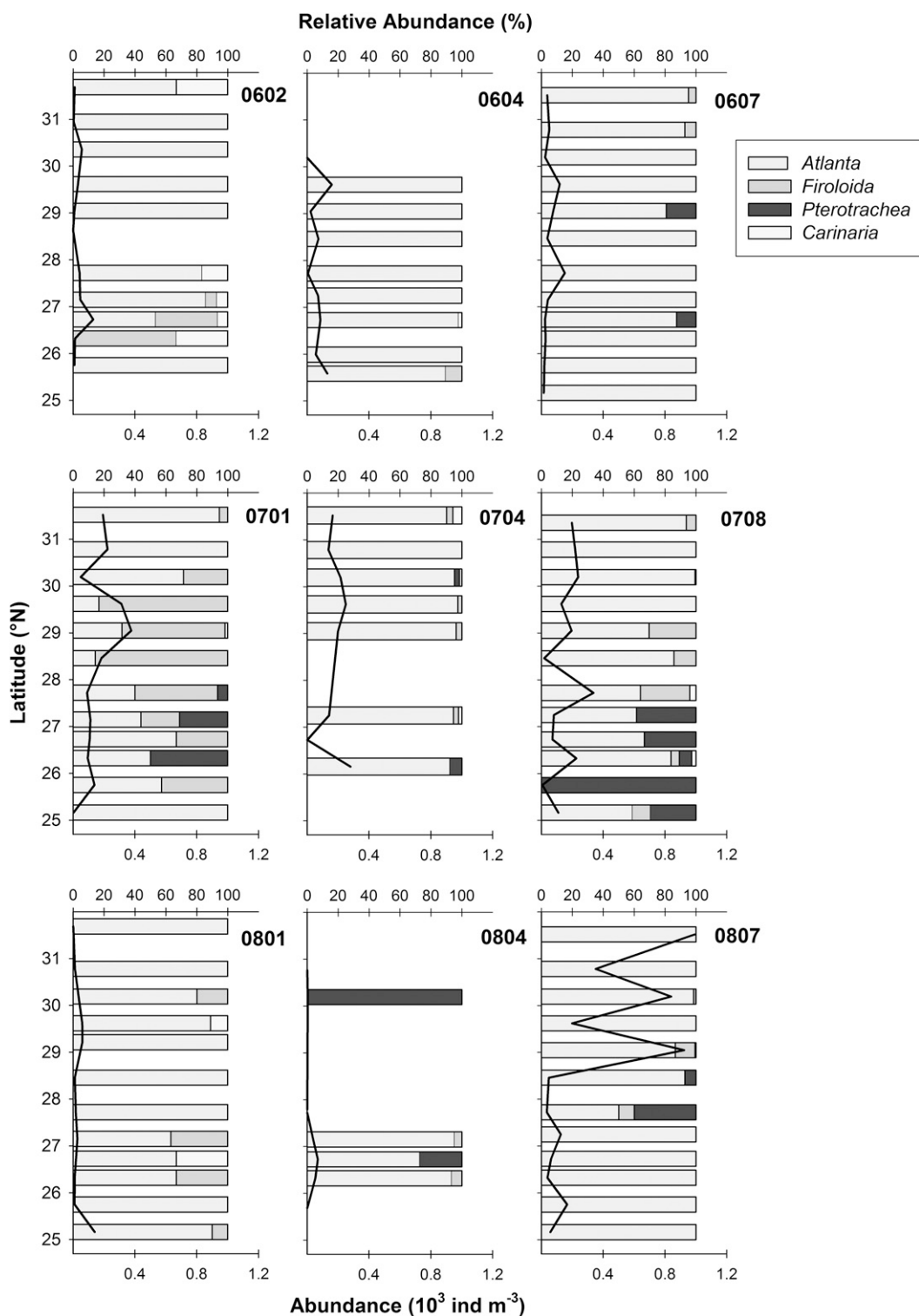
Relative Abundance (%)

Figure 7. Heteropods distribution along a latitudinal transect off the Baja California western coast during 2006-2008. Colors in bars represent relative abundance by genera and solid line is total absolute abundance.
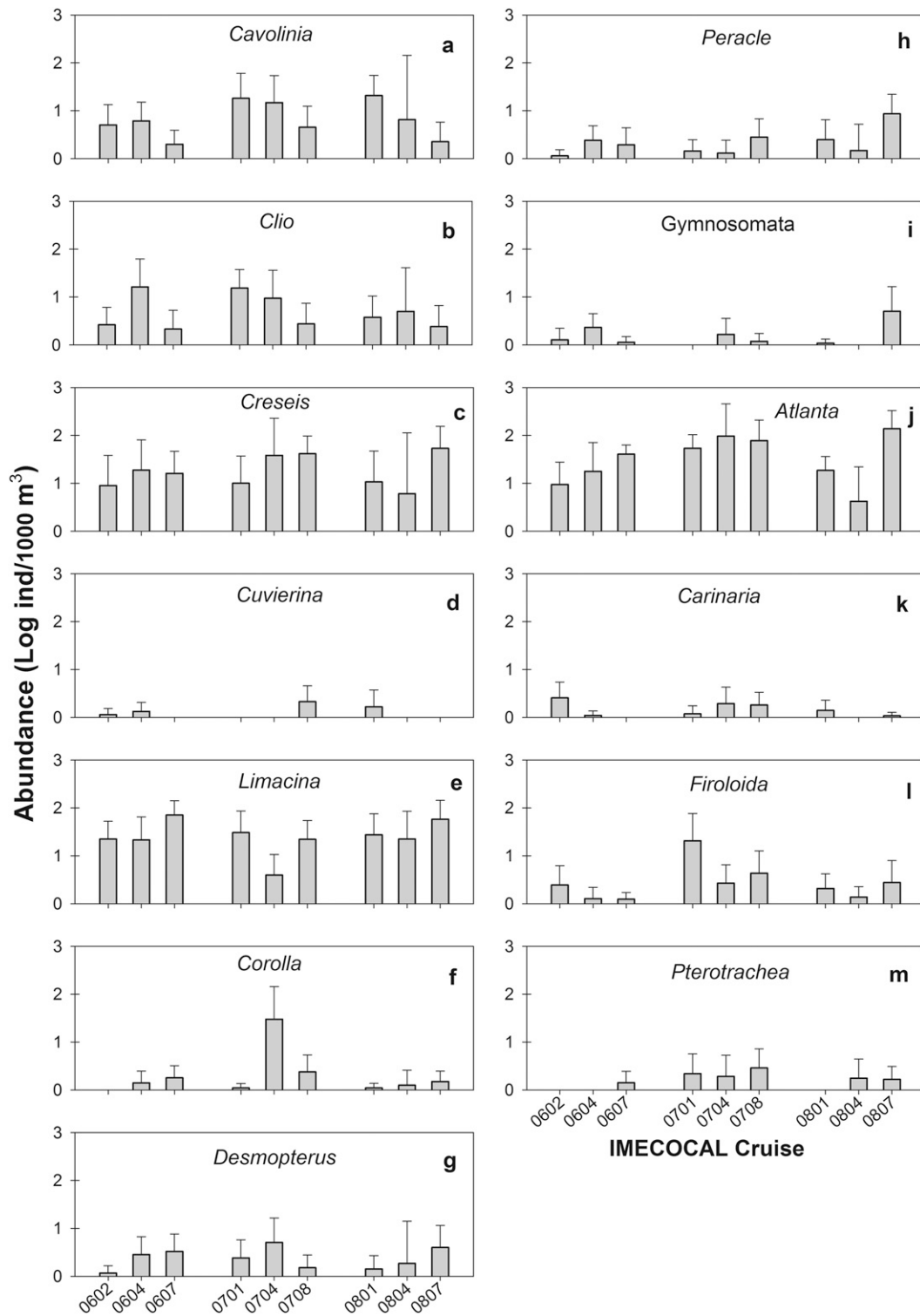
Figure 8. Mean abundance and 95% confidence interval by cruise in pteropods: Euthecosomata (a-e), Pseudothecosomata (f-h), and Gymnosomata (i); and heteropods (j-m).

Table 3. Two factor analysis of variance (month and year) for molluscan genera. Significant results are indicated by * ($\alpha = 0.05$).

	SEASON		YEAR		INTERACTION Season·Year	
Taxa	F	p	F	p	F	p
Cavolinia	8.70	<0.001*	3.77	0.027*	0.45	0.772
Clio	5.37	0.006*	1.83	0.167	1.70	0.156
Creseis	3.46	0.036*	1.17	0.314	1.69	0.160
Cuvierina	0.48	0.622	0.30	0.744	3.90	0.006*
Limacina	6.74	0.002*	3.06	0.052	1.93	0.112
Corolla	14.74	<0.001*	17.37	<0.001*	10.55	<0.001*
Desmopterus	2.57	0.082	0.26	0.774	2.20	0.076
Peracle	6.02	0.004*	2.75	0.069	2.40	0.055
Gymnosomata	3.63	0.031*	1.18	0.313	5.52	0.001*
Atlanta	8.92	<0.001*	7.91	0.001*	4.23	0.003*
Carinaria	1.44	0.242	1.93	0.151	3.64	0.009*
Firoloida	4.73	0.011*	9.43	<0.001*	1.85	0.127
Pterotrachea	1.33	0.269	4.41	**0.015**	0.35	0.843

Gymnosomata (t = 2.1, p = 0.034), while *Pterotrachea* abundance was positively related to dS (t = 2.0, p = 0.044).

Subsurface temperature was selected in preference to surface temperature. The positive sign of T_{200} coefficient could be interpreted as affinity to the California Undercurrent (CU) which is more warm and saline. However, this would be contradictory with a negative sign of S_{10} in *Creseis* (t = -2.8, p = 0.006), meaning Subarctic Water affinity. The characteristics of sampling do not allow ascertaining which one of the two currents is more critical for these taxa. Three genera had significant positive S_{10} coefficients: *Clio* (t = 2.5, p = 0.014), *Firoloida* (t = 2.7, p = 0.008), and *Pterotrachea* (t = 2.9, p = 0.005) indicating affinity for Subtropical Surface water which influences the region from the west.

Integrated chlorophyll was only selected in the models of *Creseis* and *Carinaria* (Table 4) but in *Carinaria* the regression model was not significant, while in *Creseis* the IC coefficient was not significant (p > 0.05).

DISCUSSION

Description of interannual changes in environmental conditions

During 2006-2008 abiotic conditions in the California Current system varied across seasons and years. In early 2006, SST anomalies were negative (-1 °C) in relation to the climatologic mean of 1997-2009 along the CCS (McClatchie *et al.* 2009). Negative anomalies were also observed in the equatorial Pacific, a tendency that started at the end of 2005 (Kug *et al.* 2009). Some authors considered this cooling as a La Niña event (Kug *et al.* 2009, Singh *et al.* 2011). In autumn 2006, the equatorial Pacific warmed giving way to a short and weak El

Niño, peaking in November-December of 2006, and rapidly declining in February 2007 (McPhaden, 2008). Our sampling did not capture the peak of El Niño that was in autumn 2006, but the effect was still evident in the cruise performed in January 2007. A notable episode in the study area during January and April of 2007 was an increase in salinity at the upper layer, suggesting advection of Subtropical Water from the west. This event, albeit a weak one, was considered a canonic or Eastern Pacific (EP) El Niño by some authors (see Lee and McPhaden 2010) while other authors considered the event a Central Pacific (CP) El Niño due to a relatively low magnitude of temperature, salinity, and chlorophyll anomalies (Singh *et al.* 2011, Radenac *et al.* 2012). This absence of agreement makes it difficult to interpret the biological impacts of the weak El Niño 2006-2007.

There is good agreement that after El Niño 2006-2007, the equatorial Pacific has cooled since July 2007 giving way to La Niña, which peaked in January-April 2008 (Hu *et al.* 2014). However, off Baja California, the influence of La Niña was inconspicuous in the summer of 2007 because SST anomalies were positive in relation to the period 1998-2008 (McClatchie *et al.* 2009). Those anomalies could be spurious due to a sampling bias in the summer of 2007, conducted at the end of August 2007, relative to the long-term mean of July. Seasonally, SST warms 1.5°C from July to August (for more detailed explanation see Lavaniegos *et al.* 2015). Probably the signal of La Niña in the CCS begun during late summer or autumn of 2007 but sampling was missing in autumn. By January 2008, La Niña was well defined in the study region with anomalies from -1 to -2 °C during January and April 2008. Further, the equatorial Pacific recorded a brief relaxation of La Niña during the summer of 2008 followed by a second cool pulse peaking in the winter of 2008-2009 (Hu *et al.* 2014). Off Baja California

Table 4. Multiple regression analyses of environmental variables for each mollusk genus. The number of selected variables following the stepwise forward procedure is shown. The p-level of intercept and each selected variable and values lower than 0.05 are indicated by * (N = 98). See Table 1 for predictor variables codes.

Taxa	Selected variables	Summary statistics	Model
Cavolinia	4	$R^2 = 0.264$; $F = 8.3$; $p < 0.001$*	$Y = 14.3$ ($p = 0.182$); $-0.42\,[S_{10}]$ ($p = 0.205$); $+0.20\,[T_{200}]$ ($p = 0.045$*); $-0.15\,[dT]$ ($p < 0.001$*); $-1.47\,[dS]$ ($p < 0.001$*)
Clio	4	$R^2 = 0.217$; $F = 6.5$; $p < 0.001$*	$Y = -24.5$ ($p = 0.021$*); $+0.78\,[S_{10}]$ ($p = 0.014$*); $-0.10\,[dT]$ ($p = 0.002$*); $-0.38\,[dS]$ ($p = 0.369$); $-0.21\,[dO]$ ($p = 0.010$*)
Creseis	7	$R^2 = 0.223$; $F = 3.7$; $p = 0.001$*	$Y = 40.1$ ($p = 0.006$*); $+0.10\,[T_{10}]$ ($p = 0.401$); $-1.27\,[S_{10}]$ ($p = 0.006$*); $+0.25\,[O_{10}]$ ($p = 0.050$); $0.20\,[T_{200}]$ ($p = 0.143$); $-0.03\,[dT]$ ($p = 0.802$); $-0.88\,[dS]$ ($p = 0.045$*); $-0.51\,[IC]$ ($p = 0.100$)
Cuvierina	2	$R^2 = 0.037$; $F = 1.8$; $p = 0.165$	$Y = 7.4$ ($p = 0.073$); $+0.01\,[T_{10}]$ ($p = 0.279$); $-0.23\,[S_{10}]$ ($p = 0.071$)
Limacina	5	$R^2 = 0.215$; $F = 5.0$; $p < 0.001$*	$Y = 10.7$ ($p = 0.288$); $+0.03\,[T_{10}]$ ($p = 0.375$); $-0.44\,[S_{10}]$ ($p = 0.154$); $+0.48\,[T_{200}]$ ($p < 0.001$*); $+0.36\,[O_{200}]$ ($p = 0.019$*); $-0.12\,[dO]$ ($p = 0.074$)
Corolla	3	$R^2 = 0.051$; $F = 1.7$; $p = 0.178$	$Y = 2.5$ ($p = 0.025$*); $-0.21\,[T_{200}]$ ($p = 0.035$*); $-0.23\,[O_{200}]$ ($p = 0.079$); $+0.03\,[dT]$ ($p = 0.268$)
Desmopterus	3	$R^2 = 0.151$; $F = 5.6$; $p = 0.001$*	$Y = 16.7$ ($p = 0.049$*); $-0.51\,[S_{10}]$ ($p = 0.053$); $+0.11\,[T_{200}]$ ($p = 0.152$); $-1.00\,[dS]$ ($p < 0.001$*)
Peracle	5	$R^2 = 0.275$; $F = 7.0$; $p < 0.001$*	$Y = -2.4$ ($p = 0.004$*); $-0.10\,[O_{10}]$ ($p = 0.118$); $+0.18\,[O_{10}]$ ($p = 0.018$*); $+0.27\,[T_{200}]$ ($p = 0.002$*); $+0.18\,[dT]$ ($p = 0.007$*); $-0.11\,[dO]$ ($p = 0.056$)
Gymnosomata	5	$R^2 = 0.185$; $F = 4.2$; $p = 0.002$*	$Y = 0.2$ ($p = 0.704$); $-0.07\,[T_{10}]$ ($p = 0.144$); $+0.22\,[O_{10}]$ ($p = 0.011$*); $-0.18\,[O_{200}]$ ($p = 0.076$); $-0.18\,[dO]$ ($p = 0.003$*)
Atlanta	5	$R^2 = 0.311$; $F = 8.3$; $p < 0.001$*	$Y = -2.9$ ($p = 0.009$*); $+0.09\,[T_{10}]$ ($p = 0.011$*); $+0.29\,[O_{10}]$ ($p = 0.011$*); $+0.22\,[T_{200}]$ ($p = 0.033$*); $+0.10\,[dT]$ ($p = 0.034$*); $-0.29\,[dO]$ ($p = 0.004$*)
Carinaria	2	$R^2 = 0.056$; $F = 2.8$; $p = 0.064$	$Y = 0.8$ ($p = 0.017$*); $-0.02\,[T_{10}]$ ($p = 0.251$); $-0.23\,[IC]$ ($p = 0.023$*)
Firoloida	5	$R^2 = 0.154$; $F = 3.4$; $p = 0.008$*	$Y = -29.9$ ($p = 0.004$*); $+0.85\,[S_{10}]$ ($p = 0.008$*); $+0.13\,[O_{10}]$ ($p = 0.209$); $+0.16\,[T_{200}]$ ($p = 0.098$); $-0.04\,[dT]$ ($p = 0.200$); $-0.19\,[dO]$ ($p = 0.014$*)
Pterotrachea	4	$R^2 = 0.157$; $F = 4.3$; $p = 0.003$*	$Y = -20.6$ ($p = 0.004$*); $+0.03\,[T_{10}]$ ($p = 0.180$); $+0.61\,[S_{10}]$ ($p = 0.005$*); $+0.54\,[dS]$ ($p = 0.044$*); $-0.06\,[dO]$ ($p = 0.217$)

these events were delayed, with the relaxed phase of La Niña occurring in late summer of 2008.

Though the interannual variability associated to ENSO was difficult to follow, it had a strong effect on biological productivity. Some authors recorded notable increases in chlorophyll and primary production during La Niña 2007-2008 in the equatorial Pacific (Turk *et al.* 2011, Radenac *et al.* 2012). This is expected and contrasts with low productivity during El Niño events (Turk *et al.* 2011). In the Baja California region, Gaxiola-Castro *et al.* (2010) showed that chlorophyll concentrations during 2003-2006 were very low compared to previous years (2000-2002), but that tendency reversed in 2007. In the area from Ensenada (~31.5° N) to San Quintín (~30.3° N) surface chlorophyll concentrations reached up to 4 mg · m^3 in April 2007 as is typical during upwelling events (McClatchie *et al.* 2008). Values continued to be high in the summer of 2007 (> 1 mg · m^{-3}), and again in January 2008 as the effect of La Niña were accompanied by high chlorophyll concentrations (> 2 mg · m^{-3}).

Changes in planktonic mollusk taxa during a weak El Niño and La Niña

Holoplanktonic mollusks changed in association to increasing chlorophyll during ENSO. For example, *Corolla spectabilis* recorded a strong increase during the transition from El Niño 2006-2007 to La Niña 2007-2008. The large size of *C. spectabilis* and high abundance, exert a strong grazing pressure (Silver and Bruland 1981). Blooms of *C. spectabilis* are common in the CCS, and McGowan (1967) described that it is more abundant north of Punta Eugenia during spring, shifting its distribution in summer-autumn to southern Baja California waters. In the present study, we found high fluctuation in the abundance of this species but not a clear seasonal tendency. Sánchez-Hidalgo (1989, 1994) did not record *C. spectabilis* off southern Baja California, which differs with our results probably due to a sampling limited to coastal waters by that author, while *C. spectabilis* has a mainly oceanic distribution (McGowan 1967).

Peracle, *Atlanta*, and Gymnosomata showed interannual particularities, increasing in abundance in summer 2008. Through the study period *Atlanta* reported abundances below to 260 ind/1000 m^3 excepting at the end in July 2008, when this species abundance ranged from 350 to 1000 ind/1000 m^3 in northern stations. High abundance of this heteropod was coincident with high pH values (8.0−8.3) off north Baja California during July 2008, the maximal values during the period 2006-2008 (Juárez-Colunga *et al.* 2010), probably favoring shell calcification of *Atlanta* and Thecosomata. In relation to Gymnosomata, though a shell is missing in the adult stage, their increase in July 2008 may be explained by their specialized feeding type on shelled pteropods (Lalli and Gilmer 1989).

Stratification and mollusk abundance

An inverse relationship between temperature, salinity, and oxygen gradients, with abundance was observed in most of the mollusk genera suggesting that stratification affects the habitat of these epipelagic species. Epipelagic species as *Limacina trochiformis* and *Creseis conica* are concentrated above 100 m depth (Wormuth 1981, Nigro and Seapy 2008), and could be affected by strong oxygen gradients. We have found both species in neritic waters of Baja California (unpublished data), but could be also abundant in oceanic areas. Abundances of *Limacina* showed inverse covariance with dO in regression analysis while *Creseis* showed positive covariance with surface oxygen (O$_{10}$). Vertical migrating species may be even more affected by a strong dO, as for example, *Clio pyramidata* (Nigro and Seapy 2008), which is abundant in the CCS. Mackas and Galbraith (2012) discussed the recent decrease of *C. Pyramidata* off Vancouver, Canada, in relation to acidification but also could be due to hypoxic conditions. Maas *et al.* (2012) showed that *C. pyramidata* is vulnerable to hypoxia in the eastern tropical Pacific, coinciding with our results of inverse relation between dO and *Clio* abundance off Baja California. Gymnosomata abundance also had inverse covariance with dO, consistent with observations of Seibel *et al.* (2007) on metabolism. They found variable response to low oxygen in Gymnosomata species depending on somatic constitution, with species of more gelatinous bodies being less active (p. ej. *Cliopsis* and *Thliptodon*) while *Clione* and *Pneumodermopsis* were active swimmers more sensible to low oxygen concentrations. Besides, the increase of oxygen gradient from 2006 and 2008 is consistent with the expansion of the minimum oxygen zones due to climate change (Paulmier and Ruiz-Pino 2009). Therefore, this deoxygenating process may already be affecting the pteropods.

The heteropods *Atlanta* and *Firoloida* also responded negatively to dO. This response was expected in *Atlanta* because the species in this genus are mostly epipelagic, adapted to well oxygenated waters. Some species may present short diel vertical migration (DVM), as *Atlanta peroni*, which live disperse in the upper 200 m during daylight hours and above 120 m in the night (Seapy 2008). *Atlanta peroni* probably was abundant in our samples, because it is known as a dominant species in the CCS (McGowan 1967, Sánchez-Hidalgo 1989, 1994). The vertical distribution of *Firoloida desmaresti* has been reported in epi- and mesopelagic waters but is not clear if performing DVM (Pafort-van Iersel 1983).

Abundances of other genera as *Cavolinia*, *Creseis*, and *Desmopterus* did not have significant coefficients with dO in the regression analysis, but were negatively related to dS, and *Cavolinia* and *Clio* also with dT (Table 4). Thermohaline stratification may affect to species performing DVM, as *C. inflexa* and *C. pyramidata* (Wormuth 1981, Nigro and Seapy 2008), but a stratified sampling was not performed to

demonstrate this possibility. A positive response to thermal stratification was observed in abundances of *Peracle* and Gymnosomata, despite the opposite covariance with dO.

Regional variability

Scarce differences between north and south regions were found, despite latitudinal differences in abiotic conditions. The only mollusks with regional differences were *Desmopterus pacificus* and *Pterotrachea*, the first one showing higher abundance in the northern region, congruent with the distribution observed by McGowan (1967). In contrast, *Pterotrachea* was more abundant in the southern region and specifically during 2007, suggesting the influence of El Niño event. The results for *Pterotrachea* coincided with the distribution described by McGowan (1967) for *P. coronata*, which is the most abundant of the genus *Pterotrachea* in the CCS, though there are other few abundant species (*P. hippocampus* and *P. minuta*). Certainly other mollusk species could have regional differences that were not detected at the generic level.

CONCLUSIONS

Therefore, during 2006-2008 we found evidence of seasonal changes in holoplanktonic mollusks, with significant increase from winter to summer in abundances of *Creseis*, *Limacina*, *Corolla*, *Peracle*, Gymnosomata, and *Atlanta*, and significant decrease in *Cavolina*, *Clio*, and *Firoloida*. The main interannual differences were found in five genera (*Cavolinia*, *Corolla*, *Atlanta*, *Firoloida*, and *Pterotrachea*) with significant increase in their abundances from 2006 to 2007, related to the transition from El Niño to La Niña. The chlorophyll concentration did not result a determinant predictor variable for the abundance of mollusks while the temperature, salinity, and dissolved oxygen were, particularly the vertical gradient of those variables. Latitudinal differences were limited to abiotic variables, mainly with increased temperature and decreasing oxygen at south of Punta Eugenia, while the mollusks showed scarce north-south differences, reserved to the pteropod *Desmopterus* and the heteropod *Pterotrachea*. Thus, the generic analysis has low sensitivity for spatial variability and therefore is not recommended for studies of mollusk distribution. However, the genera reflected changes relative to climatic variability and may be used as indicators of thermal and oxygen stratification in monitoring studies.

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